VOL. 201, NO. 6 THE AMERICAN NATURALIST JUNE 2023

# Social Familiarity and Spatially Variable Environments Independently Determine Reproductive Fitness in a Wild Bird

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*Submitted April 25, 2022; Accepted December 9, 2022; Electronically published April 10, 2023*

*Online enhancements:* supplemental PDF.

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ABSTRACT: The social interactions that an individual experiences are a key component of its environment and can have important consequences for reproductive success. The dear enemy effect posits that having familiar neighbors at a territory boundary can reduce the need for territory defense and competition and potentially increase cooperation. Although fitness benefits of reproducing among familiar individuals are documented in many species, it remains unclear to what extent these relationships are driven by direct benefits of familiarity itself versus other socioecological covariates of familiarity. We use 58 years of great tit (*Parus major*) breeding data to disentangle the relationship between neighbor familiarity, partner familiarity, and reproductive success while simultaneously considering individual and spatiotemporal effects. We find that neighbor familiarity was positively associated with reproductive success for females but not males, while an individual's familiarity with their breeding partner was associated with fitness benefits for both sexes. There was strong spatial heterogeneity in all investigated fitness components, but our findings were robust and significant over and above these effects. Our analyses are consistent with direct effects of familiarity on individuals' fitness outcomes. These results suggest that social familiarity can yield direct fitness benefits, potentially driving the maintenance of long-term bonds and evolution of stable social systems.

*Keywords:* sociality, spatial effects, reproductive success, familiarity, territorial neighbors, fitness.

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## Introduction

Individuals' reproductive success may depend on not only their own traits but also the external social and ecological settings they find themselves in (Snyder-Mackler et al. 2020). Social relationships can benefit fitness—for instance, when they facilitate cooperative interactions (Gokcekus et al. 2021)—but can also be costly when they lead to competition or conflict (Bebbington et al. 2017; McFarland et al. 2017; Menz et al. 2020). How and why individuals choose to tolerate, cooperate, or compete with others appear to vary across systems, but familiarity among individuals often plays a key role in shaping the balance between these phenomena (Ellis et al. 2019). Specifically, tolerance afforded through familiarity may increase rates of cooperation rather than competition and, consequently, increased fitness (Beletsky and Orians 1989; Silk 2007; Grabowska-Zhang et al. 2012*a*).

Across many taxa, familiarity (in a very simple sense, in terms of having previous associations) is a precursor for social tolerance and cooperation (Croft et al. 2006; Aragón et al. 2007). Having familiar associates in close proximity (socially and spatially) can increase each individual's fitness through more efficient division of labor (Griffiths et al. 2004). Familiarity is especially important for territorial species, because it can impact how much energy individuals allocate to defense of their areas and therefore how much they can allocate to reproduction (Eason and Hannon 1994). Often discussed in terms of the dear enemy effect, familiarity among neighbors allows for reduced aggression and conflict at the territory boundary and can even facilitate cooperation (Akçay et al.

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*American Naturalist*, volume 201, number 6, June 2023. © 2023 The University of Chicago. All rights reserved. Published by The University of Chicago Press for The American Society of Naturalists. https://doi.org/10.1086/724382

2009; Grabowska-Zhang et al. 2012*a*; Tumulty 2018; but see Müller and Manser 2007; Newey et al. 2010; Christensen and Radford 2018). In addition to—and possibly because of—benefits for defense, being raised among familiar individuals leads to higher fitness in various species of birds, mammals, and primates (Beletsky and Orians 1989; Seppä et al. 2001; Turner et al. 2020). Parents that have more familiar associates have been found to have higher reproductive success (Kohn 2017; Riehl and Strong 2018; Alberts 2019), and being around familiar individuals can even be more beneficial than being close to genetic relatives (Liebgold and Cabe 2008; Siracusa et al. 2020). Familiarity among parents can likewise influence reproductive success. For example, breeding with the same partner over time (pair fidelity) is associated with increased fecundity and survival probability (Black 1996; Culina et al. 2013, 2015*a*). Similarly, individuals who spend more time together (or are more familiar) prior to breeding have also been shown to have higher reproductive success (Martin and Shepherdson 2012; Sánchez-Macouzet et al. 2014; Culina et al. 2020). Overall, familiarity both within and among pairs seems to generally have a positive relationship with fitness outcomes, which is expected because of the supposed benefits it can bring to an individual.

As both familiarity and fitness depend on social and spatial processes, systems where individuals (1) are seasonally territorial and (2) have a constrained breeding period are particularly useful for exploring effects of familiarity on fitness, as the whole population attempts reproduction over the same season. Grabowska-Zhang et al. (2012*a*) simulated nest box intrusions in a great tit (*Parus major*) population during the breeding season to investigate whether neighbors would join (cooperate) in mobbing the intruder. They found that familiar neighbors (individuals that shared a territory boundary in past breeding seasons) were more likely to join in nest defense, demonstrating direct benefits of familiarity. In the same population, Grabowska-Zhang et al. (2012*b*) found that having familiar neighbors during the breeding season comes with fitness benefits. Males and females with more familiar neighbors or with familiar nearest neighbors had higher reproductive output. Furthermore, females with higher numbers of familiar neighbors were more likely to have larger clutch sizes (more eggs laid). Nevertheless, whether these patterns exist outside of spatial effects remained entirely unknown. Here, we expand upon this work with 15 years of additional data and a novel technique to control for spatial autocorrelation.

Although associations between familiarity and fitness appear fairly general, it is difficult to separate direct fitness benefits of familiarity (such as those hypothesized above) from other socioecological factors that may be related to these variables. For example, familiarity and success may covary indirectly: if some areas have higher habitat quality and those areas also support greater levels of familiarity, individuals inhabiting these areas may appear to benefit from having familiar neighbors when in reality there is no direct effect of familiarity per se on fitness. Similarly, an individual's success and that of its neighbors may determine whether pairs decide to breed in the same location (site fidelity; Doligez et al. 2002; Piper 2011), allowing for a possible reciprocal relationship between familiarity, success, and consistency in territory preferences. These processes could complicate observed relationships between familiarity and fitness if they go unaccounted for.

Here, we analyze data from a long-term study of breeding great tits to investigate how having a familiar partner and having familiar neighbors (individuals sharing a territory boundary in previous years) influence fitness when directly considering spatial effects. In addition to also quantifying the effect of habitat quality, we use an approach that models two-dimensional spatial patterns in the response variable (here, components of reproductive fitness) through the use of the stochastic partial differentiation equation (SPDE), which estimates and considers spatial variation in fitness (Lindgren et al. 2011; Lindgren and Rue 2015; Krainski et al. 2018). Building on suggestions from previous work (Grabowska-Zhang et al. 2012), this approach allows the social benefits to be extricated from spatially distributed drivers of fitness, thus separating the contributions of familiarity and spatial variation in regulating sociality and fitness. We then discuss how these findings may advance our understanding of the fitness benefits of familiarity and the potential consequences in terms of selection for maintaining mutually beneficial relationships and the evolution of stable social systems.

## Methods

### *Data Collection*

This work took place within the long-term study population of great tits at Wytham Woods, Oxford, United Kingdom (51°46′N, 1°20′W). Great tits form monogamous pairs and breed during the spring (April–July) almost exclusively in the 1,020 fixed-position nest boxes that are available across the 385-ha woodland. The great tit population and their breeding behavior have been monitored since the 1960s, using a standardized procedure (Perrins 1965). Great tits are a relatively short-lived species with annual adult survival of ∼50%; they typically breed once or twice (Perrins 1979). During the breeding season, nest boxes are visited to record information on the stages of each breeding attempt. Parents are identified (when nestlings are 6–14 days old) and, if previously unringed, are trapped and fitted with a unique BTO

(British Trust for Ornithology) metal leg ring. All nestlings are fitted with unique rings when they are 2 weeks old. Outside of the breeding season (September–February), extensive mist netting is carried out to additionally ring any immigrants to the woodland.

### *Data Analysis*

*Reproductive Data.* Birds breeding in nest boxes were monitored throughout the breeding season. Each breeding attempt consists of building a nest, laying and incubating eggs, and rearing offspring. Territory prospecting occurs prior to egg laying, which begins in April. Once hatched, chicks must be provisioned by both parents for the first ~5 days. At the start of the breeding season, nests were monitored weekly until eggs were found in order to record (if a single egg was found) or estimate (if more than one egg were found) lay date, defined as the date the first egg of the clutch was laid (usually, one egg is laid each day). Once incubation commenced, the clutch size was defined as the maximum number of eggs within the nest (unless a larger number was recorded in future hatch checks). Nests were then visited every other day from the predicted hatch date to accurately determine the hatch date, or the day that chicks started hatching. Parents were identified and/or ringed on days 6–15 (day 1 = hatch date), and all chicks were ringed and weighed (mean chick weight) on day 15. All nests were subsequently checked to determine the number of fledglings for each breeding attempt. Earlier lay date, larger clutch size, higher chick weight, and a higher number of fledglings are likely to represent increased fitness (McCleery et al. 2004; Browne et al. 2007).

*Determining Neighbors and Familiarity.* We used information on the spatial arrangement of occupied nest boxes to estimate individual territories. Voronoi diagrams (Thiessen polygons) were drawn around each occupied nest box that included all of the woodland area that was closer to that nest box than to any other occupied box (Schlicht et al. 2014). We then classified individuals as first-order neighbors if they shared a territory boundary (see fig. S3). Estimating territories and neighbors in this way within this and similar systems has previously been shown to be biologically meaningful in terms of population density and breeding success and to correlate with manually determined territory sizes and neighbors (Adams 2001; Wilkin et al. 2006; Grabowska-Zhang et al. 2012*b*; Schlicht et al. 2014).

We then determined whether individuals were neighbors in previous years and classified them as familiar neighbors accordingly (following methods from Grabowska-Zhang et al. 2012*b*). We excluded yearlings from analyses since they could not have familiar neighbors from previous years (but see sec. 1 in the supplemental PDF for independent analysis of the effect of age—adult vs. juvenile—on fitness). We created a variable denoting the number of male familiar neighbors and the number of female familiar neighbors each individual had; males and females of each pair were always considered separately, aligning with common practice in this study system and similar systems. If an individual in a neighboring box had not been identified, this could mean that some neighbors were wrongly assigned as unfamiliar. Consequently, our measures are conservative, as neighbors that were familiar could be assigned as unfamiliar but not the other way around (see fig. S3 for an illustrative explanation). It is known, however, that birds breeding for the first time are more likely to be unidentified in this population (Kidd et al. 2015), and these individuals, by definition, cannot have familiar neighbors. To conduct additional sensitivity analysis, we reran all of the models with the proportion of familiar neighbors out of all identified neighbors rather than the number of neighbors (table S4) and by limiting the analysis to individuals who have at least three (~50%) identified neighbors of each sex (sec. 4 in the supplemental PDF), which produced similar results. We also controlled for familiarity within the pair bond by including a binary pair familiarity variable indicating whether individuals bred together in the previous year.

We additionally included a count of the number of oak trees within 75 m of each nest box as a measure of habitat quality. Great tits provision their nestlings with caterpillars (found most abundantly on oak trees) and other insects, and variation in caterpillar availability has been associated with clutch size, growth rate, and fledging success (Tinbergen and Boerlijst 1990; Perrins 1991; Keller and van Noordwijk 1994; Nour et al. 1998; Rytkönen and Krams 2003; Tremblay et al. 2003; Lambrechts et al. 2004). Previous studies have also shown that broods raised close to oak trees have a better physical condition (Wilkin et al. 2009), and individuals in deciduous woodlands (with more oak trees) provision broods more often and more appropriately in terms of the size of the brood (Blondel et al. 1991).

Finally, we calculated the distance that each individual had traveled from the previous year by taking the distance of the most direct path between the nest box that they bred in for each year.

*Statistical Analysis.* We analyzed data on 8,823 individual adults that bred in the 58 years between 1965 to 2022. We first ran two generalized linear models (GLMMs) to understand the predictors of familiarity within the pair and among neighbors. The neighbor familiarity model included pair familiarity, age (numeric), sex, and distance traveled from the previous year as fixed effects and focal

ID, box, and year as random effects. The pair familiarity model included age (numeric), sex, and distance traveled from the previous year as fixed effects and focal ID, box, and year as random effects. To investigate the association between familiarity and reproductive success, we fitted GLMMs using the integrated nested Laplace approximation (INLA) R package, which allows for the fitting of a SPDE random effect to quantify and control for spatial autocorrelation in the response variable (Rue et al. 2009; Bakka et al. 2018; Albery et al. 2019, 2021; Martino and Riebler 2020). The SPDE effect models the distance between points to calculate spatial autocorrelation (Lindgren et al. 2011); nest box point locations and their associated reproductive output data were used to approximate spatial variation in the fitness variables. Continuous variables were scaled to have a mean of 0 and standard deviation of 1. We ran two sets of models, one with the females and another with the males, with the model structure detailed in table 1. Year is included as both a continuous fixed effect and a categorical random effect to account for any trend that has occurred over time as well as categorical yearly differences in reproductive success (Albery et al. 2019). To investigate the effect of different familiarity metrics, we iteratively added these social effects (number of familiar neighbors, number of familiar female neighbors, number of familiar male neighbors, and pair familiarity) to the base model, investigating which indicators best fit the data. We used deviance information criterion (DIC) to distinguish between models, as is often used for this analytical approach (Albery et al. 2019). In each round, we added each social effect individually and then kept the best-fitting one, until all had been added or their addition did not improve the model, using a cutoff of 2 DIC. Because the neighbor variables (overall number, male number, and female number familiar) were well correlated ($R > 0.5$), we did not allow more than one neighbor variable as explanatory variables in the same model; the models therefore sought the single best-fitting neighbor effect. In other words, we specified a separate model for each of the social fixed effects while keeping the base fixed and random effects consistent and then compared the resulting models using DIC. Fixed effect estimates were provided by the mean and 95% credibility intervals of the posterior estimate distribution. Significance was determined by examining each effect's overlap of the 2.5% and 97.5% posterior estimates with zero.

## Results

### *Familiarity Effects*

We analyzed data on individuals from 6,079 pairs. On average, each pair had five neighbors (SD = 1.53; fig. 1*A*); 82.1% of them were of known identity (SD = 19.37%), and 10.3% were familiar (SD = 15.7%). Figure 1*B* is a visual example of territories, numbers of neighbors, and familiarity in a single year (2008).

Our measures of familiarity (either within pairs or among neighbors) influenced three of the five fitness variables (i.e., were retained by the model selection process for these models; fig. 2). The models for mean chick weight and binary success were not improved by the addition of information about familiarity (tables S8, S9). Different variables were retained (through the model selection process) for males and females, leading to slightly different coefficients.

### *Pair Familiarity Effects*

Females with a familiar partner had significantly earlier lay dates (−0.109 [95% credible interval (CI), −0.155 to −0.063]) and more fledglings (0.068 [95% CI, 0.003–0.132]). Males with a familiar partner similarly had significantly earlier lay dates (−0.198 [95% CI, −0.244 to −0.152]) and more fledglings (0.075 [95% CI, 0.009–0.140]) and additionally had larger clutch sizes (0.116 [95% CI, 0.053–0.180]). These effects remained significant when controlling for spatial autocorrelation (fig. 2).

### *Neighbor Familiarity Effects*

Females with more familiar neighbors (of both sexes) had significantly earlier lay dates (−0.036 [95% CI, −0.056 to −0.015]). Females with more male familiar neighbors had significantly larger clutches (0.052 [95% CI, 0.026–0.077]; fig. 2). These effects remain when controlling for spatial

**Table 1:** Model structure

| Response (fitness) variables | Base fixed effects | Social fixed effects | Random effects |
|---|---|---|---|
| Lay date | Year | Number of familiar neighbors | Focal ID |
| Clutch size | Focal age | Number of familiar female neighbors | Year |
| Mean chick weight | Habitat quality (oaks) | Number of familiar male neighbors | SPDE (for spatially corrected models) |
| Number of fledglings |  | Pair familiarity |  |
| Binary success |  |  |  |

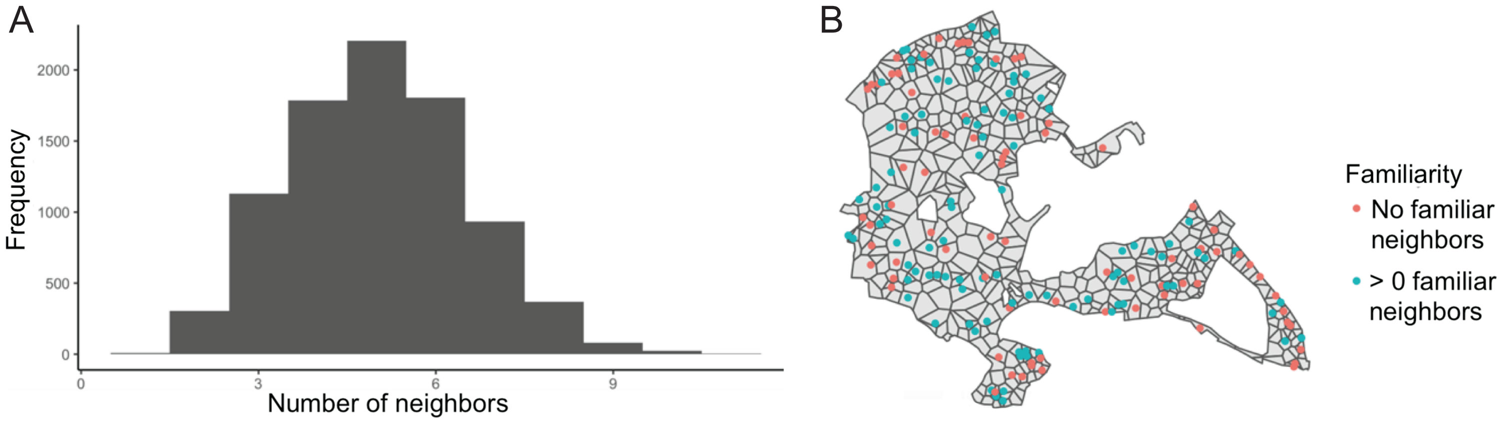

**Figure 1:** *A*, Distribution of number of neighbors pairs had. *B*, Example map from one breeding season (2008) illustrating territories, neighbors, and familiarity for individuals of known identity (by necessity restricted to birds in second year or older).

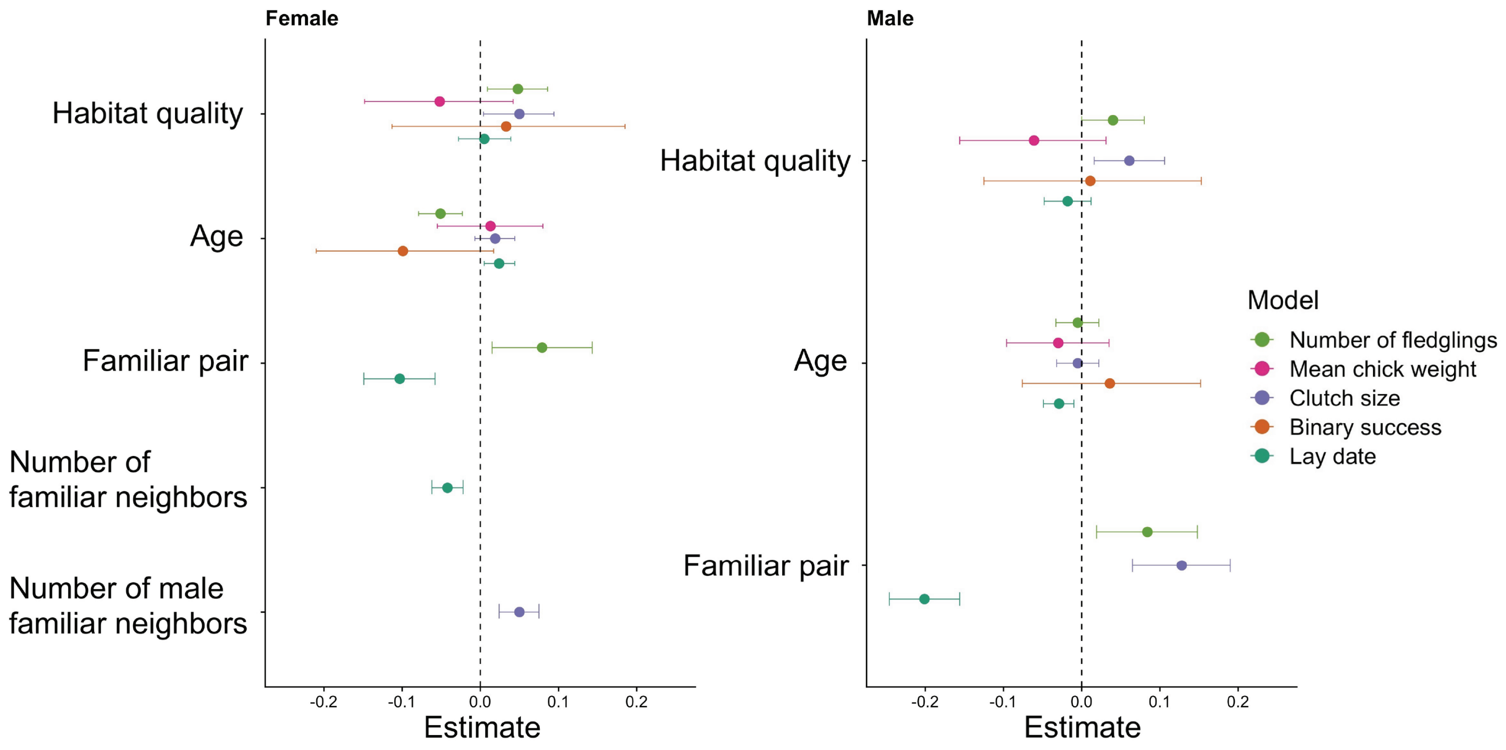

**Figure 2:** Summary (excluding intercept and year effect) of all 10 models for females and males, with SPDE spatial autocorrelation correction. Circles represent the estimate for each effect that was retained in the model selection process, and error bars denote 95% credible intervals. The same figures with the year effect included are presented in section 7 of the supplemental PDF.

autocorrelation. Further, all of the same neighbor familiarity effects are observed when considering the proportion (rather than number) of familiar neighbors (fig. S5; table S3).

### Predictors of Familiarity

The number of familiar neighbors an individual had was influenced by the distance that it had moved from the box it bred in during the previous year, with those that traveled further having fewer familiar neighbors ($z = -19.99$, $P < .001$; table 2, pt. A). It was rare for familiarity to arise from individuals just remaining in identical breeding locations in successive years. Specifically, overall only 1.92% (SD = 1.41%) of dyads were familiar because neither move boxes from the previous year. Furthermore, when the models are run with the additional control variable of whether individuals stayed in the same box as the previous years, the results largely hold (sec. 5 in the supplemental PDF). As expected, familiar pairs also had more familiar neighbors ($z = 3.01$, $P < .001$). In terms of familiarity within the pair, older individuals ($z = 3.36$, $P < .001$) and those that traveled shorter distances ($z = 18.81$, $P < .001$) from their box in the previous year were more likely to be familiar with their partner (table 2, pt. B).

### Environmental Drivers

For females, better habitat quality was associated with significantly earlier lay dates (−0.069 [95% CI, −0.091, −0.047), larger clutches (0.062 [95% CI, 0.031–0.092), heavier mean chick weight (0.058 [95% CI, 0.014–0.131), and more fledglings (0.049 [95% CI, 0.020—0.079), but the effect remained significant only for number of fledglings in the spatially corrected models (0.048 [95% CI, 0.009–0.086; fig. 2). For males, better habitat quality was associated with significantly earlier lay dates (−0.077 [95% CI, −0.098 to −0.057), larger clutch size (0.065 [95% CI, 0.037–0.094), and a higher number of fledglings (0.045 [95% CI, 0.017–0.074), but once spatial autocorrelation was controlled for, the effect remained significant only for clutch size (0.063 [95% CI, 0.016–0.109; fig. 2).

Table 2: GLMM results for predictors of pair familiarity and number of familiar neighbors, with individual ID, box, and year included as random effects

| Response and variable | Estimate | SE | Z | P |
|---|---|---|---|---|
| A. Number of familiar neighbors: | | | | |
| Intercept | .050 | .050 | .999 | .318 |
| Pair familiarity (true) | .076 | .025 | 3.011 | <.001 |
| Age | .010 | .011 | .854 | .393 |
| Sex (male) | .004 | .023 | .166 | .868 |
| Distance traveled from previous year | −.478 | .024 | −19.991 | <.001 |
| B. Pair familiarity: | | | | |
| Intercept | −1.381 | .114 | −12.169 | <.001 |
| Age | .102 | .030 | 3.360 | <.001 |
| Sex (male) | .124 | .061 | 2.016 | .044 |
| Distance traveled from previous year | −1.400 | .074 | −18.813 | <.001 |

To graphically illustrate the spatial distribution of each of the fitness variables when accounting for the fixed and random effects in each model, we projected the SPDE random effect onto a two-dimensional plane (figs. 3, S8; method explained further in sec. 5 in the supplemental PDF). The projections for females (fig. 2) and males (fig. S8) differ slightly but follow the same pattern. Generally, fitness metrics are lower in the southern part of the woods. When considering the northern portion of the woods, those in the western part have earlier lay dates (2A), larger clutches (2C), and a higher number of fledglings (2E). The entire northern portion has relatively high chick weight (2D), while binary success has a more patchy distribution (2B). Accounting for spatial autocorrelation improves all of the models substantially (table 3).

### Base Model Effects

In all 10 of the models (tables S8, S9), year was a significant predictor of all of the fitness variables, and this was still the case once spatial autocorrelation was controlled for (fig. 2). There were several significant effects of age: older females had later lay dates (0.022 [95% CI, 0.002–0.042) and fewer fledglings (−0.049 [95% CI, −0.077 to −0.020), while older males had earlier lay dates (−0.034 [95% CI, −0.054 to −0.014). When accounting for spatial autocorrelation, the effects remained the same.

Without accounting for the effects of familiarity, we also compared adult versus juvenile success (figs. S1, S2; tables S1, S2). For females, adults had significantly earlier lay dates (−0.096 [95% CI, −0.110 to −0.083) and larger clutches (0.099 [95% CI, 0.081–0.116). Adult males had significantly earlier lay dates (−0.084 [95% CI, −0.098 to −0.070), larger clutches (0.056 [95% CI, 0.036–0.076), more fledglings (0.034 [95% CI, 0.014–0.054), and a higher chance of success (0.084 [95% CI, 0.005–0.166). When accounting for spatial autocorrelation, the effects remained the same but adult females also had significantly more fledglings (0.022 [95% CI, 0.002–0.041).

## Discussion

Using 58 years of data documenting breeding success and territorial neighbor familiarity in a wild bird population, we demonstrate how pair and neighbor familiarity

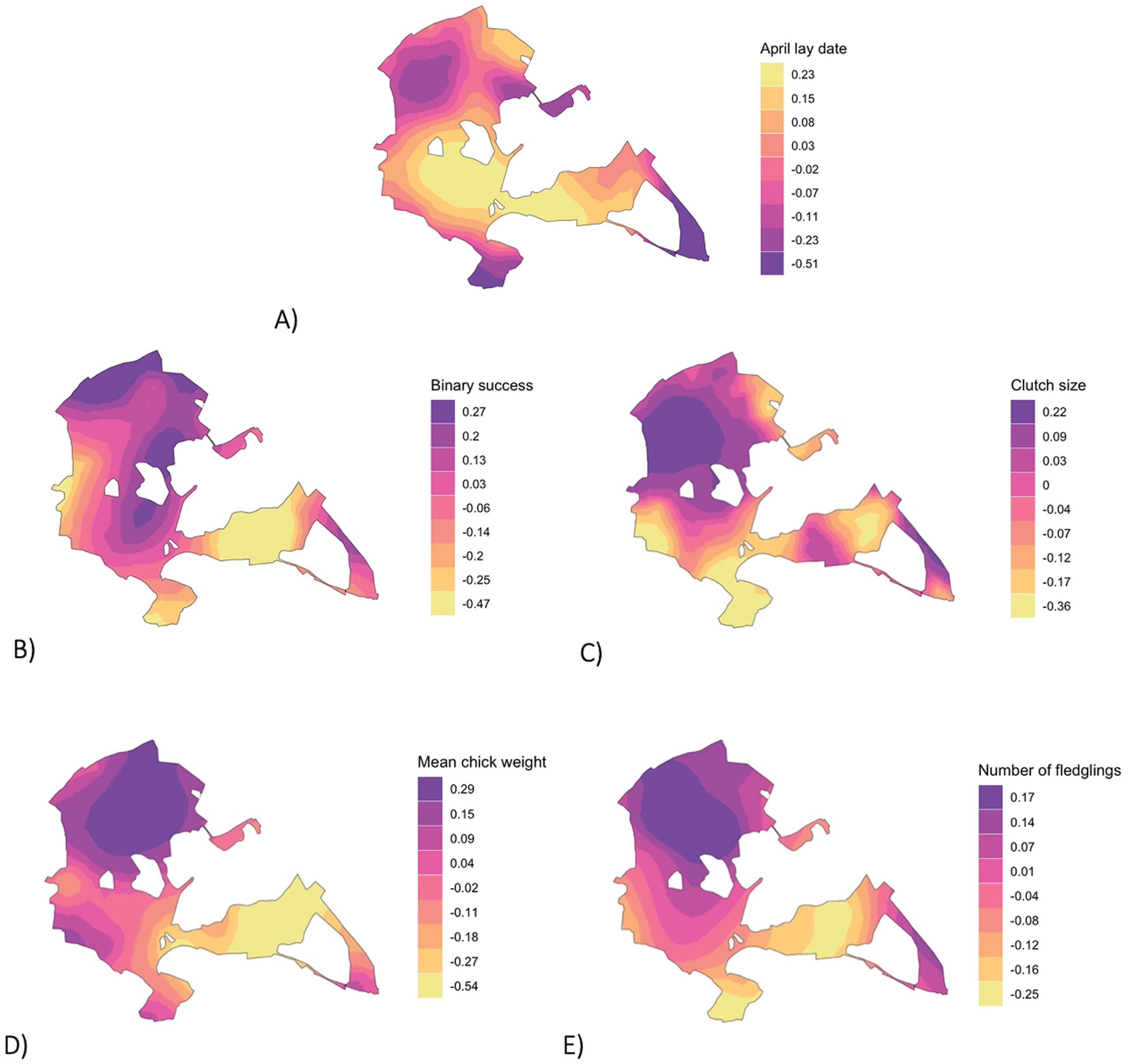

**Figure 3:** Two-dimensional projection of spatial distribution of each fitness variable (with *z*-scores) for females, when accounting for fixed and random effects in each model, onto actual map of study area. The method for projection is further explained in section 5 of the supplemental PDF.

influence reproductive success and how this operates over space. We find that familiarity within pairs and among neighbors increases reproductive success, confirming benefits of neighbor familiarity for females in terms of earlier lay dates and larger clutches. This work builds on previously established findings in this population (Grabowska-Zhang et al. 2012*b*), which had previously suggested these patterns but could not separate the potentially confounding effects of spatial autocorrelation and pair familiarity. Here, by replicating these findings using more than a decade of additional data, additionally considering familiarity within the pair, and accounting for a variety of environmental confounders, we provide evidence for the standalone importance of neighbor familiarity. Importantly, we largely replicate the results (particularly for clutch size) while additionally accounting for spatial heterogeneity in our fitness variables. Expanding upon these previous findings, we highlight that this relationship is not just the product

**Table 3:** DIC for base and SPDE models

| Sex and model | Base | SPDE | ΔDIC |
|---|---|---|---|
| Male: | | | |
| Lay date | 8,314.272 | 8,165.894 | −149.377 |
| Binary success | 2,347.758 | 2,337.212 | −10.545 |
| Clutch size | 11,647.945 | 11,525.877 | −122.067 |
| Mean chick weight | 2,215.621 | 2,165.770 | −49.851 |
| Number of fledglings | 12,013.903 | 11,929.604 | −84.299 |
| Female: | | | |
| Lay date | 7,626.573 | 7,479.224 | −147.349 |
| Binary success | 2,156.470 | 2,143.878 | −12.593 |
| Clutch size | 10,214.466 | 10,143.980 | −70.487 |
| Mean chick weight | 2,050.142 | 2,022.038 | −28.104 |
| Number of fledglings | 11,291.936 | 11,245.623 | −46.312 |

of an indirect covariation in space but also due to a direct benefit.

Overall, pair familiarity influenced lay date, clutch size, and number of fledglings, and neighbor familiarity was related to lay date and clutch size. Pair familiarity was associated with higher reproductive success for both sexes; females additionally benefited from having familiar neighbors, while males did not. Although all fitness distributions were heavily autocorrelated in space, the effects of familiarity persisted over and above this spatial heterogeneity. Our results demonstrate the importance of social factors as well as spatial factors in determining reproductive outcomes. It is well documented that social instability can come with negative effects in terms of survival (Herzog et al. 2009; Capitanio and Cole 2015; Maldonado-Chaparro et al. 2018); here we show that maintaining stable social relationships, particularly for females, is important for reproductive success.

The strongest fitness effect we identified was that of pair familiarity, with familiar pairs being more successful overall and both males and females in familiar pairs having a higher number of fledglings than those in unfamiliar pairs. This may be in part driven by the propensity of unsuccessful individuals to divorce or change their breeding partner (Culina et al. 2015*b*). Previous work has shown that pairs in this population also benefit from spending more time with each other in the winter prior to the breeding season, because this behavior allows for earlier lay dates (Culina et al. 2020). This is the first time that other ecological variables that could create these patterns have been considered; our findings likewise demonstrated earlier lay dates (and increased fitness) in familiar pairs, suggesting that stronger bonds both within and between years contribute to increased reproductive success, partially by facilitating earlier laying. Similar results have been found in other monogamous avian species (Black 2001; Van De Pol et al. 2006; Griggio and Hoi 2011; Gabriel and Black 2013; Sánchez-Macouzet et al. 2014; Wiley and Ridley 2018; Leach et al. 2020; Maldonado-Chaparro et al. 2021) but not in others (Naves et al. 2007; Hatch and Westneat 2008). It is possible that previously observed effects of neighbor familiarity on fledging success in this population (that we do not find here) may have been driven by a lack of accounting for familiarity within the pair (Grabowska-Zhang et al. 2012).

A variety of proximate mechanisms of neighbor familiarity could underlie their observed fitness effects. Because traits like lay date and clutch size are predominantly controlled by the female (Browne et al. 2007; Evans et al. 2020), it is perhaps unsurprising that females rather than males benefit from having familiar neighbors. Females with more familiar neighbors have earlier lay dates, which may arise from their ability to avoid disputes and acquire territories earlier in the season. Females with more male familiar neighbors lay larger clutches; this was also found by Grabowska-Zhang et al. (2012). This may be due to a perception of increased food security in terms of the ability to forage more widely (Nicolaus et al. 2009). Females may also have extrapair copulations with those familiar males (Beck et al. 2020). Importantly, higher-quality females may acquire more familiar neighbors while also producing larger broods, driving apparent between-individual correlations between neighbor familiarity—for example, if individuals choose associates on the basis of their apparent quality. Although extrapair paternity is estimated to be relatively low in this populations (13%–14%; Blakey 1994; Patrick et al. 2012), further work considering genetic paternity and rates of extrapair copulations is needed to gain a better understanding of the relationship between neighbor familiarity, extrapair copulations, and fitness outcomes.

Accounting for the structure of spatial autocorrelation significantly improved all of the models. Different fitness components had slightly different distributions, but the northern portion of the woods tended to feature higher fitness than the others (fig. 2). This pattern may be driven by the fact that the southern portion has a higher number of nest boxes available or because it is slightly closer to roads and urban areas (rather than farmland), but further work is necessary to determine the precise drivers of this spatial variation (Perrins and Jones 1974). There were also strong effects of habitat quality on some variables (clutch size and number of fledglings) that were in addition to the spatial variation observed. This suggests that habitat quality or spatial effects alone cannot account for the observed benefits of familiarity. Similarly, it is encouraging that the social effects we observed were likewise robust to accounting for spatial effects, particularly given that social structure and behavior are themselves dependent on environmental drivers (He et al. 2019).

The benefit that comes with maintaining social relationships may contribute to cooperation among nonkin. This becomes more pertinent as individuals age, as favoring relationships with familiar individuals can counter the negative effects of senescence on survival and reproduction (Roper et al. 2021) within (Nicolai et al. 2012; Culina et al. 2013) and/or outside of (Silk et al. 2010; Kohn 2017; Siracusa et al. 2020) the pair. As is the case for other studies on the relationship between familiarity and fitness, our findings are limited to the particular context and environment that is investigated. The costs and benefits of familiarity are likely to vary across species and across different environments in terms of climate, density, or predation risk (Brask et al. 2019; Liu et al. 2020; Capilla-Lasheras et al. 2021). Future similar studies across different populations could help to tease apart these effects. Furthermore, while current analytical techniques (such as INLA SPDE effects employed here) often assume that spatial effects are consistent over time, further work could examine the temporal stability of spatial effects and how they may vary with other ecological factors. Understanding temporal patterns of changes in spatial effects and covariation with ecology would further develop our understanding of the relationship between time, space, and sociality. Finally, it is unclear whether individuals actively choose to stay in similar areas so that they have familiar neighbors or whether individuals that stay close to their initial breeding location just happen to have more familiar neighbors (although birds in this population do have stronger overwinter bonds with their future neighbors; Firth and Sheldon 2016). To unravel causality in this setting, future studies could examine reproductive success while manipulating (by either limiting or encouraging) dispersal distances and/or the ability to recouple with one's mate. Identifying the fitness benefits of familiarity and delineating it from its spatial correlates in this way will further inform the factors driving the evolution of sociality and cooperation.

## Acknowledgments

We thank all individuals who contributed to the long-term data collection of Wytham Woods' great tit population monitoring. This work was supported by grants from the Biotechnology and Biological Sciences Research Council (BB/L006081/1, BB/S009752/1), European Research Council (AdG250164), and Natural Environment Research Council (NE/K006274/1, NE/S010335/1, NE/V013483/1).

## Statement of Authorship

S.G., J.A.F., and B.C.S. were responsible for conceptualization. J.A.F. and B.C.S. acquired the funding. Data analysis, model analysis, and visualization were carried out by S.G. and G.F.A. S.G. wrote the original draft, and all other authors provided supervision and reviewed and edited the manuscript.

## Data and Code Availability

All data and code have been deposited in the Dryad Digital Repository (https://doi.org/10.5061/dryad.7m0cfxpzc; Gokcekus et al. 2023).

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Associate Editor: Michael J. Sheehan
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